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FUNCTIONAL NICHE PARTITIONING IN THERIZINOSAURIA PROVIDES NEW INSIGHTS INTO THE EVOLUTION OF THEROPOD HERBIVORY

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Abstract: Dietary specialisation is generally considered to be a crucial factor in driving morphological evolution across extant and extinct vertebrates. The ability to adapt to a specific diet and to exploit ecological niches is thereby influenced by functional morphology and biomechanical properties. Differences in functional behaviour and efficiency can therefore allow dietary diversification and the coexistence of similarly adapted taxa. Therizinosauria, a group of secondarily herbivorous theropod dinosaurs, is characterised by a suite of morphological traits thought to be indicative of adaptations to an herbivorous diet. Digital reconstruction, theoretical modelling and computer simulations of the mandibles of therizinosaur dinosaurs provides evidence for functional niche partitioning in adaptation to herbivory. Different mandibular morphologies present in therizinosaurians were found to correspond to different dietary strategies permitting coexistence of taxa. Morphological traits indicative of an herbivorous diet, such as a downturned tip of the lower jaw and an expanded post-dentary region, were identified as having stress mitigating effects. The more widely distributed occurrence of these purported herbivorous traits across different dinosaur clades suggests that these features also could have played an important role in the evolution and acquisition of herbivory in other groups.

Key words: functional niche partitioning, finite element analysis, Dinosauria, herbivory, functional morphology

Niche partitioning is a viable mechanism among sympatric species to allow the coexistence of similarly adapted taxa and to minimise competition for resources (MacArthur 1972; Chase & Leibold 2003; Finke & Snyder 2008). With regard to diet, niche partitioning can act upon food type, habitat, foraging time and foraging behaviour (Schoener 1974; Patterson *et al.* 2003; Adams & Thibault 2006). These differentiations are directly influenced by how and how efficiently taxa can exploit available resources, and dictated by physiological, anatomical, and functional properties. Differences in functional morphology and the ability to adapt to a different diet, such as herbivory, can therefore allow the occupation of new or further subdivision of existing ecological niches. Consequently, the acquisition of herbivory has often been considered an important key innovation and has been acquired numerous times in vertebrate evolutionary history (Sues 2000). Within Dinosauria, herbivory has evolved convergently in Ornithischia, Sauropodomorpha and Theropoda (Barrett *et al.* 2011; Barrett 2014). In the latter, the adaptation to an herbivorous diet represents a departure from the carnivorous condition of most basal theropods, which occurred presumably independently in Oviraptorosauria, Ornithomimosauria and Therizinosauria (Barrett 2000, 2005; Zanno & Makovicky 2011), and appears to have been a major driver for morphological diversity and speciation in theropods.

Therizinosauria, a group of herbivorous theropods predominantly found in Cretaceous sediments of Asia and North America, has a complicated taxonomic history and their unusual skeletal morphology has long obfuscated their phylogenetic position (Clark *et al.* 2004). Derived members of this group are characterised by small skulls with an edentulous

premaxilla and a rostral rhamphotheca, an elongate neck, hypertrophied manual unguals and a broad, opisthopubic pelvis (Zanno 2010a; Lautenschlager *et al.* 2014). This mosaic of morphological features resulted in a variety of phylogenetic hypotheses (Barsbold & Perle 1984; Paul 1984; Gauthier 1986) and it was not until the discovery of new fossils that Therizinosauria was firmly established as a derived clade within Theropoda (Russel & Dong 1993).

Within the last two decades a number of new fossil findings have further substantiated the phylogenetic position of therizinosaurians (Zanno 2010a; Averianov 2015). These new discoveries revealed that therizinosaurians were more widely distributed across North America and Asia than originally thought. Furthermore, the coeval occurrence of different taxa and morphotypes within the same locality (Sues & Averianov 2016; Zanno *et al.* 2016) indicates that different species might have occupied different ecological niches. While the skeletal morphology of Therizinosauria is strongly divergent from that of other theropods, it is also very diverse across different therizinosaurian species. In particular, tooth morphology, claw shape and body size were found to be highly variable, presumably reflecting different palaeoecological specialisations and herbivorous dietary strategies among Therizinosauria (Zanno 2010a; Zanno & Makovicky 2013; Lautenschlager 2014).

However, while the increasing number of newly discovered taxa have significantly improved knowledge of therizinosaurians, the often fragmentary nature of many specimens have not only confounded phylogenetic analyses, but also comprehensive understanding of their anatomy, palaeobiology and palaeoecology. In particular cranial remains are rare and only few skeletal elements are equally represented in all taxa. Amongst them, the dentary is the most consistently preserved element known from at least six therizinosaurian taxa (Fig. 1). It shows a high degree of morphological variation and characteristic features, such as a downturned symphyseal region, rostral edentulism, and a lateral shelf, all of which are

thought to be indicative of dietary specialisation patterns (Zanno & Makovicky 2011). Furthermore, lower jaw elements are ideally suited for biomechanical studies, as the mandible is primarily adapted for foraging and biting, whereas the cranial skeleton represents a compromise of multiple functions (e.g., bony housing of brain and sensory systems). Still, the problem remains that fragmentary preservation, taphonomic artefacts and the availability of specimens preclude comprehensive biomechanical studies (Zanno 2010a).

The use of theoretical, virtual models can provide a versatile solution. While kinematic abstractions have been used to model theoretical and actually realised jaw morphologies in dinosaurs in the past (e.g. Weishampel 1984, 1998), high computational demands considerably limited the necessary complexity of such models. Recent advances in hard- and software technology now allow the simulation of complex and thus more realistic models. Consequently, the use of biomechanical analysis techniques in palaeontological research using approaches, such as finite element analysis (FEA), has increased in recent years, but theoretical modelling of anatomical features has been used only in a handful of studies (Rayfield & Milner 2008; Anderson *et al.* 2011; Xing *et al.* 2015). Although it involves the use of idealised models, which do not reflect the fossil morphology completely, recent studies have attested this approach to be very informative (Bright 2014; Rahman & Lautenschlager *in press*) as it allows studying morphofunctional properties unimpeded by preservation and taphonomic artefacts.

Using actually preserved specimens as well as theoretical models, the functional morphology of the dentary (and as far possible also the complete mandibles) of six therizinosaurian species were investigated with biomechanical analysis techniques. The complete and well-preserved mandibles of the derived therizinosaurid *Erlikosaurus andrewsi* was employed as a template to create theoretical models incorporating morphological information provided by fossil specimens of other taxa, spanning the full phylogenetic and

morphological range across Therizinosauria (Fig. 1). The biomechanical behaviour and performance of different dentary morphologies was studied using FEA to test for possible dietary and functional specialisations of Therizinosauria within the herbivorous regime. The combined use and integration of actually preserved specimens and theoretical models helped overcome limitations posed by the incomplete fossil record and to evaluate the functional morphology of mandibular characters associated with herbivory. This approach further allowed testing the hypothesis that functional niche partitioning permitted the coeval diversification of taxa and the refinement of dietary strategies, thereby elucidating the evolutionary dynamics of ecological partitioning and the evolution of herbivory in theropod dinosaurs.

MATERIAL AND METHODS

Institutional abbreviations

HGM, Henan Geological Museum, China; IGM, Geological Institute of the Mongolian Academy of Sciences, Ulaanbataar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA.

Specimens and model creation

The complete mandible of the therizinosaurid *Erlikosaurus andrewsi* (IGM 100/111) was used as a template for the creation of the digital models. The specimen was digitised at X-Tek Systems (now Nikon Metrology) using a XT-H-225ST CT scanner with parameters set at 180kV and 145µA. Slice data consisting of 1998 slices with a slice thickness of 145 µm were imported into Avizo (versions 6.3.1.and 7.0.0; VSG, Visualization Science Group) for

image segmentation and further processing. Moderate digital restoration was necessary to remove preservational artefacts, such as small breaks and cracks (Lautenschlager *et al.* 2014).

The digitally restored model of the mandible of *Erlikosaurus andrewsi* was subsequently modified to create mandible models of five further therizinosaurian taxa for which the dentary is known: *Falcarius utahensis* (UMNH VP 14527, 14528 and 14529) (Zanno 2010b), *Beipiaosaurus inexpectus* (IVPP V11559) (Xu *et al.* 1999), *Jianchangosaurus yixianensis* (HGM 41HIII-0308A) (Pu *et al.* 2013), *Alxasaurus elesitaiensis* (IVPP 88402) (Russel & Dong 1993), and *Segnosaurus galbinensis* (IGM 100/80) (Zanno *et al.* 2016). For that purpose all mandibular elements of *Erlikosaurus andrewsi* were imported into the 3D modelling and visualisation software Blender (www.blender.org) as .obj files. Photographs in different orientations derived from personal observations (*Falcarius utahensis, Beipiaosaurus inexpectus*) and from published figures of the dentary and (where preserved) other mandibular elements of the above listed taxa were imported as reference images in Blender. Using the mesh manipulation tools in Blender, the models of *Erlikosaurus andrewsi* were each modified: The outlines of the digital models were fitted to the morphology of the reference images in different views. Individual elements were scaled, rotated and translated to correspond to the shape of the specific modelled taxa (Rahman & Lautenschlager *in press*). Where necessary, different components, such as teeth, were duplicated and placed as indicated by the reference images. In taxa for which the postdentary morphology is unknown (*Falcarius utahensis, Alxasaurus elesitaiensis*), only the dentary was modelled in the way described above. Postdentary elements were supplemented unchanged (except for uniformly scaling to match the size of the dentary) from the *Erlikosaurus* models. This step assumes that the respective taxa shared a similar postdentary morphology, which might not correspond to the actual condition. However, the supplemented postdentary elements provide attachment for the dentary and thereby allow analysing the preserved morphology. Results for the

postdentary morphology of *Falcarius utahensis* and *Alxasaurus elesitaiensis* might therefore reflect these assumptions and are treated accordingly. The final models were remeshed using Blender's remeshing modifier and exported as .stl files for FEA.

Finite element analysis

For FEA, all models were scaled to the same surface area (based on the mandible of *Erlikosaurus andrewsi*) to remove size-related effects during analyses (Dumont *et al.* 2009) and imported into Hypermesh (version 11, Altair Engineering) for the creation of solid mesh FE models. All models consisted of approximately 1,500,000-2,000,000 four-noded tetrahedral elements (see supplementary table 1). Material properties for crocodilian bone and teeth were assigned in Hypermesh (bone: E = 20.49 GPa, n = 0.40; teeth: E = 60.40 GPa, n = 0.31) and treated as homogenous and isotropic following (Creech 2004; Chen *et al*. 2008). A keratinous rhamphotheca covering the premaxilla and the rostral part of the dentary had been reconstructed in *Erlikosaurus andrewsi* (Lautenschlager *et al.* 2013, 2014) and is thought to be present in some derived therizinosaurid. However, such a rhamphotheca was not incorporated in the current FE models, as basal therizinosaurians most likely lacked this structure (Zanno 2010b). While the presence of a keratinous sheath has been shown to mitigate stress and strain in the underlying bone (Lautenschlager *et al.* 2013), further sensitivity tests demonstrated that a keratin cover only changed the magnitude but not the distribution of stress and strain (Lautenschlager 2014; Lautenschlager *et al*. 2016). Similarly, sutures between the individual mandibular elements were not included. The inclusion of cranial sutures in FE models can have an effect on stress and strain magnitudes (e.g. Bright & Gröning 2011, Porro *et al.* 2011; Reed *et al.* 2001; Bright 2012), but material properties of cranial sutures in archosaurs are often poorly known (Porro *et al.* 2013, Cuff *et al.* 2015),

However, in a comparative context as employed here, these factors can be assumed to affect all models equally so that it is possible to extract shape as the crucial parameter only.

All FE models were restrained from rigid body movement in all directions at the articular (15 constraints). Further constraints were applied according to the tested functional scenarios (see below). Muscle loads were applied at the mandibular insertions according to the reconstructed jaw adductor arrangement for *Erlikosaurus andrewsi* (Lautenschlager 2013), with a total of 569 N applied to each hemi-mandible (supplementary table 2). *Each muscle group was modelled as a series of loads to represent and cover the extent of the attachment area.* Muscle forces and locations were kept constant for all models to allow analysis of shape in a comparative context. Although it is likely that some variation in muscle arrangement and mass existed in the different taxa, a conservative approach was taken here. This approach avoids the introduction of functional variance due to different loading properties, which would mask mechanical differences due to mandibular shape. All models were subsequently imported into Abaqus (version 6.10, Simulia) for analysis and postprocessing. Biomechanical performance was assessed by comparison of von Mises stress and strain distribution. In addition, reaction forces were obtained from the solved FE models at the bite points. Ratios between input forces and output forces and average von Mises stress values were calculate to quantify biomechanical efficiency. Variation in deformation for each model and loading scenario was quantified using a landmark-based approach (for the undeformed and deformed models). Twenty-six landmarks were placed at morphologically homologous points (supplementary fig. 11) using Avizo and subjected to Procrustes superimposition and a principal component analysis (PCA) performed in PAST (Hammer *et al.* 2001).

Simulated feeding scenarios

To analyse ecomorphological differences between taxa, a variety of feeding scenarios was simulated: (i) unilateral biting at the first, fifteenth and last tooth with single constraints applied at the respective positions. The fifteenth tooth position was chosen as it represents the average midpoint of the tooth row; (ii) bilateral biting at the first, fifteenth and last tooth position, with single constraints applied accordingly; (iii) clipping of an object at the tip of the dentary with a single constraint at the centre of the dorsal margin of the symphysis; (iv) upwards-pull movement, which simulates grasping of an object at the tip of the dentary and pulling dorsally. An additional load (150 N) was applied at the symphyseal region in dorsal direction; (v) a downwards-pull movement, which simulates the grasping of an object at the tip of the dentary and pulling ventrally. An additional load with a magnitude within the range of the bite force (150 N) was applied at the symphyseal region in ventral direction; (vi) lateral pull, simulating sideways movement while holding an object at the rostral teeth. An additional load (150 N) was applied at the symphyseal region in lateral direction.

RESULTS

Stress distribution

As postdentary elements are unknown in some taxa and were extrapolated on the basis of the preserved material of *Erlikosaurus andrewsi*, results largely focus on the dentary. The comparison of the stress and strain distributions obtained from FEA demonstrates distinct differences between the analysed mandibular models. *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* show the lowest stress and strain levels in the dentary but also the complete mandible during unilateral and bilateral bite scenarios (Fig. 2, supplementary figs. 1-7) simulating biting at the first, middle and last tooth positions. In comparison, the models of *Jianchangosaurus yixianensis* and *Alxasaurus elesitaiensis* experience the highest stress and strain levels (Fig. 2, supplementary figs. 2, 3). If only the dentaries are considered,

Falcarius utahensis, *Jianchangosaurus yixianensis* and *Alxasaurus elesitaiensis* show the highest stress magnitudes. In all models the dentary shows the relatively lowest stress magnitudes during unilateral and bilateral biting, with stress hotspots centred on the angular and articular region. Stress in the dentaries is mostly focused on the ventral surface for biting at the first and middle tooth position, but shifts posteriorly to the postdentary elements when simulating a bite at the last tooth. Stress magnitudes are moderately higher on the balancing side, whereas stresses are reduced and more uniformly distributed on both sides in the bilateral biting scenarios (supplementary fig. 4). The same patterns are observed for strain and deformation distributions (supplementary figs. 5-7) throughout all models.

In addition to different bite positions, further functional scenarios were analysed simulating clipping at the tip of the dentary, and the mandible pulling an object in dorsal, ventral and lateral direction as would be experienced during foraging. Among these, clipping models experience the lowest stress levels throughout the mandible, but considerably higher levels than biting at the first, middle and last tooth (Fig. 3, supplementary fig. 8). Increased stress levels are induced in the symphyseal region for simulated clipping. As with the different biting scenarios, *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* show the lowest stress magnitudes in the mandibles during clipping (Fig. 3). The same patterns, however, are also observed, if only the dentaries are considered.

Among the extrinsic scenarios with additional forces applied to the mandible to simulate pulling of an object in different directions, the upwards-pull scenario produces the highest stress and strain magnitudes for all models (Fig. 3, supplementary figs. 8-10), with stress and strain hotspots found around the articular region. In comparison, the lateral-pull scenario produces slightly lower, but still high levels of stress and strain. In this scenario, stress hotspots are centred on the lateral surface of the dentary in addition to the postdentary elements (Fig. 3). A downwards pull movement shows the relatively lowest stress and strain

levels (supplementary figs. 8-10). Stresses are mostly concentrated on the ventral surface of the dentary, the angular and the articular regions. For all extrinsic feeding scenarios, the mandibles of *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* show the lowest stress and strain levels, whereas the highest magnitudes were generally observed in *Jianchangosaurus yixianensis* and *Alxasaurus elesitaiensis*. If only the dentaries are considered, *Erlikosaurus andrewsi*, *Segnosaurus galbinensis* and to a lesser degree *Beipiaosaurus inexpectus* experience the lowest stress magnitudes during the extrinsic feeding scenarios. The calculation of average von Mises stress for all models is consistent with these results obtained from the contour plots (Fig. 4A): *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* have the lowest per-element average stress values for both the intrinsic and extrinsic scenarios. In contrast, average von Mises stress is highest in *Falcarius utahensis* and *Alxasaurus elesitaiensis*, confirming the aforementioned observations of the contour plots quantitatively.

Relative bite forces

Relative bite forces obtained from the FE models reveal considerable differences in how muscle forces are translated into bite forces among the studied taxa. As expected, relative bite forces increase with a posterior shift of the bite position, due to the skull acting as a third-class lever. *Alxasaurus elesitaiensis* records the highest relative bite forces for biting at the first (23-32% of muscle force), middle (27-35%) and last tooth position (56-66%) (Fig. 4B). Relative bite forces for *Falcarius utahensis* fall within the same, although somewhat lower range (first tooth: 19-24%, middle tooth: 23-27%, last tooth: 43-59%). By comparison, *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* possess the lowest relative bite forces ranging from 14-18% (first tooth), to 20-27% (middle tooth) and maximally 28-38% (last tooth) (Fig. 4b).

Functional morphospace

Principal component analysis (PCA) plots obtained from the morphometric analysis of the undeformed and deformed mandible models illustrate the biomechanical behaviour of the different morphologies in response to functional scenarios (Fig. 5, supplementary fig. 12). PC axes 1 and 2 account for over 70% variation in deformation of the mandibular models. PC 1 correlates with the dorsal displacement of the posterior dentary and postdentary region, whereas PC 2 represents the displacement in mediolateral width (i.e. mandibles draw closer together moving along positive axis). Although a large overlap exists between the individual models and functional scenarios (Fig. 5), differences in the degree of deformation are visible. *Alxasaurus elesitaiensis* (8%) and *Beipiaosaurus inexpectus* (12%) occupy relatively smaller regions of the morphospace, whereas *Jianchangosaurus yixianensis* (32%) and *Erlikosaurus andrewsi* (33%) show the highest degree of morphospace occupation.

DISCUSSION

The combination of digital reconstruction, theoretical modelling and biomechanical analysis demonstrates the functional diversity of therizinosaurian mandibles. As attested by the results obtained from FEA, differences in mandibular morphology correlate with different functional behaviours and likely reflect dietary specialisation patterns within this group of herbivorous theropods.

Considerable differences in mechanical performance (stress and strain magnitudes, relative bite forces, deformational variation) between the modelled taxa suggest distinctive morphofunctional trends. For all tested loading scenarios, the dentary and complete mandibular morphologies of *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* were found to experience the lowest stress and strain magnitudes (but also the lowest relative bite forces). Both taxa differ from other therizinosaurians in the dorsoventrally expanded

299 postdentary and coronoid region. An elevated coronoid eminence is frequently found in
300 herbivorous dinosaurs and is a uniting feature of Ornithischia, culminating in prominently
301 heightened coronoid processes in derived groups, such as ceratopsids and hadrosaurids
302 (Ostrom 1961; Upchurch *et al.* 2004; Weishampel 2004; Bell *et al.* 2009; Tanoue *et al.*
303 2009). While it has been demonstrated that the elevation and expansion of the coronoid
304 region is mechanically beneficial by increasing moment arms and mechanical advantage
305 (Nabavizadeh 2016), further stress reducing effects have been hypothesised by providing an
306 enlarged surface for ligamentous tissues (Bell *et al.* 2009). As observed here, the dorsolateral
307 expansion of the postdentary and coronoid region appears to provide additional stress
308 mitigating benefits. However, it should be noted that the postdentary elements of *Falcarius*
309 *utahensis* and *Alxasaurus elesitaiensis* are unknown. It is therefore possible that these taxa
310 might have possessed similar morphological adaptations to mitigate stresses. Comparing the
311 results for the dentaries of the analysed taxa only suggests a similar pattern. The ventrally
312 curved and downturned symphyseal region in *Erlikosaurus andrewsi* and *Segnosaurus*
313 *galbinensis* experience lower stress and strain magnitudes, in particular for the extrinsic
314 feeding scenarios. Additionally, the symphyseal region of the dentary in *Erlikosaurus*
315 *andrewsi* (and possibly also in *Segnosaurus galbinensis)* was likely covered by a keratinous
316 sheath (Lautenschlager *et al.* 2014), which has been shown to further mitigate stress and
317 strain magnitudes (Lautenschlager *et al.* 2013). Among Therizinosauria (and other
318 herbivorous coelurosaurs), a downturned and convex symphyseal region of the dentary has
319 been assumed to be a primary adaptation to herbivory (Zanno & Makovicky 2011). By
320 comparison, the elongate and straight dentary morphologies of *Falcarius utahensis*,
321 *Jianchangosaurus yixianensis*, and *Alxasaurus elesitaiensis* record the highest stress and
322 strain magnitudes. This indicates that the relatively unmodified jaw morphology
323 reassembling the plesiomorphic coelurosaurian and dinosaurian condition (Langer 2004;

Choiniere *et al.* 2010) offers less stress resistance. This may seem surprising, considering basal coelurosaurs were adapted to carnivory. However, within hypercarnivorous clades, including Tyrannosauroidea, a trend towards the dorsoventral expansion of the postdentary and coronoid region in derived members is observable, which might likely have served the same stress mitigating purpose (Holtz 2004; Holtz *et al.* 2004; Eddy & Clarke 2011). Although prone to increased stresses, the mandible models of *Falcarius utahensis* and *Alxasaurus elesitaiensis* produced the highest relative bite forces amongst the analysed therizinosaurian taxa. This suggests that the elongate mandibular morphologies could represent a compromise between high bite forces and increased stress susceptibility. However, in *Falcarius utahensis* and *Alxasaurus elesitaiensis* the tooth row extends relatively closer to the jaw joint, resulting in higher bite forces.

The observed differences in mandibular robustness and relative bite forces indicate dietary adaptations and specialisations across the individual therizinosaurian taxa and functional diversification in the course of their evolution. The basal-most therizinosaurian *Falcarius utahensis* is characterised by high relative bite forces, moderate stress and strain magnitudes, in particular during unilateral and bilateral biting scenarios, and moderate deformational variation as indicated by the functional morphospace occupation. Although the exact timing of a shift from carnivory to herbivory in Therizinosauria is difficult to identify, the osteology of *Falcarius utahensis* suggests that this dietary transformation was not yet fully completed at this stage (Zanno 2010b). It is therefore possible that *Falcarius utahensis* retained relatively high bite forces in order to sustain an omnivorous life style. In more derived therizinosaurians, relative bite forces were found to be considerably lower. This pattern indicates that these taxa might have engaged in less oral processing and instead relied on other means to process vegetation, such as gut fermentation or gastric mills (although unambiguous evidence for the latter has not been found) (Zanno & Makovicky 2011; Zanno

et al. 2009), whereas the low bite forces were compensated for by harnessing the postcranial musculature to crop foliage (Lautenschlager *et al.* 2013). As aforementioned, though, the observed differences in relative bite forces are partially influenced by the length and extent of the tooth row, leading to relatively higher bite forces in *Falcarius utahensis*, *Jianchangosaurus yixianensis* and *Alxasaurus elesitaiensis*.

Low stress and strain magnitudes in *Beipiaosaurus inexpectus* and *Erlikosaurus andrewsi* show that these taxa would have been more flexible in their foraging behaviour as they were able to engage in different feeding styles without increasing stress levels, which could have been further mitigated by the presence of a keratinous sheath (Lautenschlager *et al.* 2013). Although scarce for the majority of therizinosaurian deposits, preserved plant fossils demonstrate the palaeoenvironment of *Beipiaosaurus inexpectus* to be diverse and abundant in conifers, ferns and bennettitaleans (Zhou *et al.* 2003). Results from the extrinsic loading scenarios would further suggest that a downwards pull motion while gripping vegetation is generally more likely for all studied taxa than a lateral or upwards movement. However, taxa with a downturned symphyseal region (*Erlikosaurus andrewsi*, *Segnosaurus galbinensis*), which mitigates stresses in the dentary during lateral pulling, could have been more likely to engage in this behaviour. In contrast, the increased stress levels found for a pull-upwards scenarios for all taxa indicate foraging of vegetation at head level, but not below. These findings are consistent with the functional morphology of the postcranial skeleton. The trend towards increased neck length in derived therizinosaurians indicates the importance of extending the browsing range (Zanno 2010b), whereas the manual unguals of most taxa had been adapted for grasping vegetation during foraging (Lautenschlager 2014). In contrast, the claws of *Alxasaurus elesitaiensis* were found to have been used in a more generalist fashion (Lautenschlager 2014), which is reflected also in the results for the

mandibular function here, suggesting that this species was ecologically more flexible in comparison to other therizinosaurians.

For the sympatric taxa *Erlikosaurus andrewsi* and *Segnosaurus galbinensis* the differences in relative bite force show that *Segnosaurus galbinensis* would have been able to feed on tougher vegetation, whereas overall robustness in *Erlikosaurus andrewsi* suggests a greater flexibility in feeding style as stress levels stay low across different feeding simulations. Adaptation to coarser and tougher food has been shown to be a common, but not exclusive mechanism for niche separation in contemporaneous herbivorous dinosaurs (Fiorillo 1998; Mallon & Anderson 2014). Specialisations in tooth morphology found in *Segnosaurus galbinensis* support the assumption that both taxa were functionally adapted to different foraging behaviour and food selection (Zanno *et al.* 2016). Differentiations of the dentary teeth in *Segnosaurus galbinensis* hint at increased incorporation of the dentition on procuring or processing food, whereas previous findings for *Erlikosaurus andrewsi* demonstrate that this species mostly employed the rhamphotheca as a cropping device, whilst harnessing the neck musculature during foraging (Lautenschlager *et al.* 2013). Actual size differences between the two taxa (estimated mass: *Erlikosaurus* ca. 174-278 kg, *Segnosaurus* ca. 1469 kg; Lautenschlager *et al.* 2012; Zanno & Makovicky 2013) suggest that these effects were likely increased and hint at additional mechanisms of resource partitioning such as height stratification (Bakker 1978; Weishampel & Norman 1989; Zanno & Makovicky 2013; Mallon *et al.* 2013). However, considering that many therizinosaurian taxa are more widely separated by time and geography, other factors than intra-clade competition were likely at work in driving biomechanical variability within Therizinosauria. Adaptive responses to different floras and competition with other herbivores might have been a further factor in shaping morphological diversity.

A number of morphological traits thought to be indicative of an herbivorous diet have been identified in Therizinosauria, many of which are also more broadly distributed across Coelurosauria (Zanno & Makovicky 2011; Barrett 2014), such as a downturned symphyseal region of the dentary, an elevated coronoid region, rostral edentulism and modifications of tooth shape. Results from the present study thereby offer the chance to evaluate the functional significance of these purported herbivorous characters, allowing general statements to be made regarding the evolution of theropod herbivory in general.

As demonstrated by the results, *Falcarius utahensis* differs considerably from other therizinosaurians in possessing relatively high bite forces and moderate stress and strain levels, consistent with its basal position and the retention of some plesiomorphic characters (e.g. elongate, straight mandible, symphyseal teeth). Following this initial stage, a rapid morphological and functional diversification within Therizinosauria took place, manifested in a general decrease of bite forces and the evolution of stress mitigating characters, such as an extended postdentary region and a downturned symphyseal region of the dentary. This trend is paralleled by rostral edentulism and the development of a keratinous rhamphotheca covering the tip of the dentary and skull, which has been shown to provide additional stress reducing effects (Lautenschlager *et al.* 2013). Similar morphological trajectories can be observed in other herbivorous theropod clades (e.g. Ornithomimosauria, Oviraptorosauria) and ornithischians (e.g. Ceratopsia, Ankylosauria, Stegosauria), in which comparable characters have evolved (Ostrom 1966; Barrett *et al.* 2011; Zanno & Makovicky 2011; Mallon & Anderson 2013; Barrett 2014). Features, such as a characteristically downturned dentary, have classically been proposed as primary adaptations to herbivory and are widely distributed across herbivorous dinosaurs (Sues 2000; Zanno & Makovicky 2011;Barrett 2014; Novas *et al.* 2015) and some archosauromorphs more generally (Flynn *et al.* 2010). Furthermore, the expression of a downturned dentary has recently been demonstrated to be

linked to a dietary shift from omnivory to herbivory with ontogeny in the theropod dinosaur *Limusaurus inextricabilis* (Wang *et al.* 2016). Results obtained here suggest that the presence of this feature provides a viable mechanism for stress mitigation in herbivorous taxa confirming long-held assumption about its functionality (e.g Barrett 2000, 2014 and references therein). The acquisition of additional stress-reducing structures, such as a keratinous sheath covering the symphyseal region of the dentary and the rostrum of the skull, further indicates the importance of bracing the rostral region of the snout. With a shift from a faunivore to a plant-based diet, the functional focus moves from the tooth row to the rostralmost part of the skull and lower jaw as a device for procuring food. As a consequence, this region is being reinforced through the development of a downturned dentary and the acquisition of a keratinous sheath in herbivorous theropods and many ornithischians. A comparable mechanism can be found in sauropods, in which a dorsoventral expansion of the symphyseal region has been shown to achieve the same effect of reducing stresses (Button *et al.* 2016). This convergent evolution of morphologically and functionally similar features suggests that these anatomical modifications of the mandible convey an important biomechanical advantage for herbivorous taxa.

CONCLUSIONS

As shown in this study, the combined use of digital reconstruction, theoretical modelling and biomechanical analysis techniques provides powerful tools to overcome preservational limitations of the fossil record and to study the functional significance of morphological variation of skeletal structures. Using this approach, different mandibular morphologies present in therizinosaurian dinosaurs were found to correspond to different dietary strategies permitting niche-differentiation and coexistence of taxa. Morphological features indicative of an herbivorous diet, including a downturned tip of the lower jaw and an expanded post-

dentary region, were identified as having stress mitigating effects. The more widely distributed occurrence of these purported herbivorous traits in other theropod and dinosaur clades further suggests that these features played an important role in the evolution and acquisition of (dinosaur) herbivory. However, while some morphofunctional trends can be identified using the therizinosaurian dataset, a larger sample size is necessary to further disentangle the functional significance of herbivorous characters and their individual contribution.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: doi:10.5061/dryad.vd68s

[FIG S1. Comparison of displacement distribution for different unilateral biting scenarios in studied therizinosaurian mandibles.

FIG S2. Comparison of maximum principal strain distribution for different unilateral biting scenarios in studied therizinosaurian mandibles.

FIG S3. Comparison of minimum principal strain distribution for different unilateral biting scenarios in studied therizinosaurian mandibles.

FIG S4. Comparison of Von Mises stress distribution for different bilateral biting scenarios in studied therizinosaurian mandibles.

FIG. S5. Comparison of displacement distribution for different bilateral biting scenarios in studied therizinosaurian mandibles.

FIG. S6. Comparison of maximum principal strain distribution for different bilateral biting scenarios in studied therizinosaurian mandibles.

FIG. S7. Comparison of minimum principal strain distribution for different bilateral biting scenarios in studied therizinosaurian mandibles.

FIG. S8. Comparison of displacement distribution for different feeding scenarios in studied therizinosaurian mandibles.

FIG. S9. Comparison of maximum principal strain distribution for different feeding scenarios in studied therizinosaurian mandibles.

FIG. S10. Comparison of minimum principal strain distribution for different feeding scenarios in studied therizinosaurian mandibles.

FIG. S11. Landmark positions for geometric morphometrics analysis

FIG. S12. Deformational variation of tested mandibular models and loading scenarios. Principal component plot based on geometric morphometric analysis of undeformed and deformed models.

SUPPLEMENTARY TABLE 1. Number of tetrahedral elements (rounded to the nearest 10,000) for the different FE models

SUPPLEMENTARY TABLE 2. Muscle forces applied to the different mandible models.

SUPPLEMENTARY MODEL 1. 3-D model of *Falcarius utahensis* in STL format.

SUPPLEMENTARY MODEL 2. 3-D model of *Jianchangosaurus yixianensis* in STL format.

SUPPLEMENTARY MODEL 3. 3-D model of *Beipiaosaurus inexpectus* in STL format.

SUPPLEMENTARY MODEL 4. 3-D model of *Alxasaurus elesitaiensis* in STL format.

SUPPLEMENTARY MODEL 5. 3-D model of *Erlikosaurus andrewsi* in STL format.

SUPPLEMENTARY MODEL 6. 3-D model of *Segnosaurus galbinensis* in STL format.]

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FIGURE CAPTIONS

FIG. 1. Reconstructed therizinosaurian mandibles shown in phylogenetic context. Preserved elements depicted in light grey and missing elements depicted in dark grey in lateral outline images. All models scaled to the same surface area. Phylogeny simplified after Zanno (2010a).

[intended for 110 mm two-thirds page width]

FIG. 2. Comparison of von Mises stress distribution for different unilateral biting scenarios in studied therizinosaurian mandibles. (A) *Falcarius utahensis*, (B) *Jianchangosaurus yixianensis*, (C) *Beipiaosaurus inexpectus*, (D) *Alxasaurus elesitaiensis*, (E) *Erlikosaurus andrewsi*, (F) *Segnosaurus galbinensis*. From left to right, bite point at first, middle and last tooth position indicated by arrows. Scale bar represents 100 mm.

[intended for 166 mm full page width]

FIG. 3. Comparison of von Mises stress distribution for different feeding scenarios in studied therizinosaurian mandibles. . (A) *Falcarius utahensis*, (B) *Jianchangosaurus yixianensis*, (C) *Beipiaosaurus inexpectus*, (D) *Alxasaurus elesitaiensis*, (E) *Erlikosaurus andrewsi*, (F) *Segnosaurus galbinensis*. From left to right, clipping at tip of dentary, pulling downwards, upwards and lateral. Direction of pull indicated by arrows. Scale bar represents 100 mm.

[intended for 166 mm full page width]

FIG. 4. Quantitative assessment of biomechanical differences for tested mandibular models and loading scenarios. (A) Average von Mises stress. (B) Relative bite forces (calculated as

ration between input and output forces). Range of values in each graph derived from unilateral and bilateral bite simulations.

[intended for 80 mm column width]

FIG. 5. Deformational variation of tested mandibular models and loading scenarios. Size of individual morphospace correlates with the degree and extent of deformation subjected to loading. Principal component plot based on geometric morphometric analysis of undeformed and deformed models. PC 1 correlates with the dorsal displacement of the posterior dentary and postdentary region, PC 2 represents the displacement in mediolateral width (i.e. mandibles draw closer together moving along positive axis). Filled circles represent undeformed models.

[intended for 110 mm two-thirds page width]